Journal of the Royal Society of Western Australia, Vol. 67, Part 2, 1985, p. 59-65.

Acacia cyclops G. Don (Leguminosae-Mimosaceae) in Australia: Distribution and Dispersal

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Manuscript received 22 November 1983; accepted 17 April 1984.

Abstract

Acacia cyclops is a shrub found along the coast of southwestern Australia and of mediterranean-climate South Australia. Within its natural distribution, *A. cyclops* was associated with naturally- and artificially-disturbed habitats. Reproduction occurred only by seed. Regionally, human dispersal for horticulture and revegetation projects has occurred across thousands of kilometres. Locally, birds have distributed the seed in regurgitated pellets or in faeces. Pellets were usually associated with feeding sites while faeces were common under perches and near watering points. Seed moved in these ways was found less than 200 m from the nearest mature bush. Secondary dispersal of seeds by six ant species was observed. Ants left seeds on the surface or took it into their nests: dispersal distances were less than 2 m. Seed-feeding bugs were common in the litter beneath bushes but absent from bare ground. Higher temperatures experienced by seeds on bare ground are likely to enhance germination. Dispersal away from canopies onto bare ground may allow successful establishment because of reduced predation and enhanced chances of germination and establishment.

Introduction

Like many species which have become pests in alien lands, *Acacia cyclops* A. Cunn. ex G. Don, a native of Australia, has been studied more in South Africa than in its homeland. This shrub was introduced into South Africa in the 1850s as a sand binder (among a number of purposes) but was so successful it became a pest in the fynbos vegetation of the Cape (Roux 1961, Shaughnessy 1980). The present study began in order to compare and contrast the ecology of *Acacia cyclops* in the two countries where seed dormancy and behaviour appear to differ (Gill 1981). This report attempts to provide an ecological perspective of the species within Australia. Specifically, it is concerned with the distribution and dispersal of the species, both locally and regionally.

Distribution

Acacia cyclops is usually found as a spreading shrub up to 4 m in height. It may also occur as a low-profile shrub in exposed locations along the coast or as a small tree up to 6 m tall. Its distribution has been gleaned from records of herbaria in Perth, Adelaide and Canberra as well as by personal observation. Typically, the species is found in coastal localities but has been recorded up to 60 km from the sea at Jerramungup (between Albany and Esperance) in southwestern Australia. It is known from localities just north of Jurien Bay on the Indian Ocean, and at many coastal localities to the south and east through to Kangaroo Island in South Australia (S.A.) on the Southern Ocean.

The entire range of the species is in the winter rainfall zone where frosts are rare and summers are warm and dry. Much of the climatic range of the species is encompassed by the "mediterranean" designation but *A. cyclops* also occurs in very dry conditions at the head of the Great Australian Bight. Average annual rainfall at Eyre over a three year period was less than 300 mm (Congreve 1982) while at William Bay near Denmark, Western Australia (W.A.), the mean annual rainfall is between 1 150 and 1 270 mm (Commonwealth of Australia 1962).

Calcareous sands are a feature of the occurrence of *A. cyclops* in the Perth area where some aspects of zonation have been mentioned by Seddon (1972), Smith (1973) and Powell and Emberson (1981). The species is not confined to calcareous substrates, however. It occurs on siliceous sands at Point Culver, W.A. (Nelson 1974), on ironstone gravel near middle Mt. Barren, W.A. (annotation on Perth specimen collected by R. A. Saffrey October 1970), in heavy red clay near Jerramungup (annotation on Perth specimen collected by Tindale and Maslin, March 1970) and in cracks between granite boulders outcropping from the sea at Two Peoples Bay Nature Reserve, W.A.

These broad features of distribution represent only part of the framework of this species' tolerance: an important missing local element is the positive effect of certain levels of disturbance on distribution. Mapping the appropriate types and levels of disturbance across the present distributional range is not yet possible but the common occurrence of *A. cyclops* on naturally and artificially disturbed ground can be illustrated by the following example.

At remote Eyre on the Great Australian Bight, *A. cyclops* was found on the 300 m wide calcareous erosion pavement inland of the miniature dune at the head of the beach. Frequency of occurrence was greater on the inland side of the pavement and on the more stable of the recently mobile dunes which abutted it. The species was rare on the long-stable dunes supporting mallee eucalypts although one 6 m tall specimen was found on an eroding remnant. The cause(s) of mobility of these dunes and their colonization are not known. Geologically, however, this part of the Roe Plain must have had mobile dunes repeatedly during its formation and as the sea retreated.

Historically, too, mobile dunes have been a feature of the Roe Plain as noted by the explorer Eyre (1845). Whether or not settlement and rabbit invasion exacerbated this situation is unknown. Aerial photos available from 1941 to the present show an increase in the area of mobile dunes over the past 40 years or so.

While *A. cyclops* at Eyre was associated with what appeared, at least in part, to be a natural erosion-sediment cycle, the species in many other localities was commonly associated with human disturbance. At Two Peoples Bay Nature Reserve near Albany, the species was found along the commonly travelled roads, on old vehicle tracks now disused, around the picnic area and close to the most frequently used areas of the bayside beach.

Christensen and Kimber (1975) noted that *Acacia cyclops* was "rarely subject to fire". At Eyre there was no evidence of fire at all and on the dunes there was insufficient fuel to carry a fire. Near Perth, however, fires—usually small in area—have occurred in areas of *Acacia cyclops* especially where fuels were influenced by the presence of exotic grasses. Mature *Acacia cyclops* was readily killed by fire.

Dispersal

Natural dispersal of seed of *Acacia cyclops* was studied mainly at Perth and at Two Peoples Bay. A little supplementary data on bird dispersal of seed was collected at Cape le Grand National Park near Esperance, W.A. Because the species has horticultural value in Australia and has been exported, enquiries were made of seed merchants in Perth and of CSIRO Division of Forest Research in Canberra regarding their dispersal of seed. In Perth, one of the major merchants was the Forests Department of the Western Australian Government. Their records showed the sale of seed from W.A. to S.A. and to various plant nurseries in southwestern Australia. Seed from W.A. and S.A. has been sent by CSIRO to a number of countries including Yugoslavia, India, United States of America, Mexico, the Sudan, Egypt, Ajibouti, Iran, Malta, Chile and Madagascar. Historically, the carriage of seed to South Africa has already been mentioned: it is of interest that seed of *A. cyclops* arrived in South Africa via Europe (Shaughnessy 1980).

Natural dispersal of *Acacia cyclops* was strongly influenced by the presence of the bright red aril encircling the shiny black seed. The seed itself had an average dry weight of about 25 mg while the aril weighed about half this. The seed contained an average about 12% oil but the aril contained 40% (O'Dowd and Gill, unpublished) thereby being an excellent nutritional source. When the fruit, a legume, dehisced in late spring or summer the seeds were exposed but held on the plant by the aril—thereby presenting a colourful display of red/black dispersal units. Potentially, the seeds could remain on the plant for long periods because the legumes persisted for a year or two before deteriorating and falling: actually, the seeds may be removed quickly by dispersers or fall of their own accord before most legumes fall.

Five types of post-dispersal units could be distinguished on the ground at Two Peoples Bay Nature Reserve. They were the seed-plus-aril, the seed alone and three aggregate structures. The last three were cylindrical, of bird origin, and distinguished on the basis of diameter (Fig. 1) viz. 2-3 mm, 4-9 mm and 12-15 mm. The smallest diameter units were bird faeces typically with one seed; the medium diameter units, also faeces, usually contained about 8 seeds; the largest units were regurgitated pellets and had and average of 38 seeds each (Fig. 2). Each type of aggregate often contained materials unrelated to *Acacia cyclops*: the smallest units had mostly very small seeds as well as the single large *Acacia* seed, while the other units often contained insect remains and some other seeds. The smallest dispersal units were consistent with being the faeces of silvereyes (*Zosterops lateralis*), small birds weighing about 9 g, medium units with faeces of red wattlebirds (*Anthochaera carunculata*) or other medium to large avian dispersers (see below) and the largest with regurgitated pellets of grey currawongs (*Strepera versicolor*)—large birds weighing about 400 g.

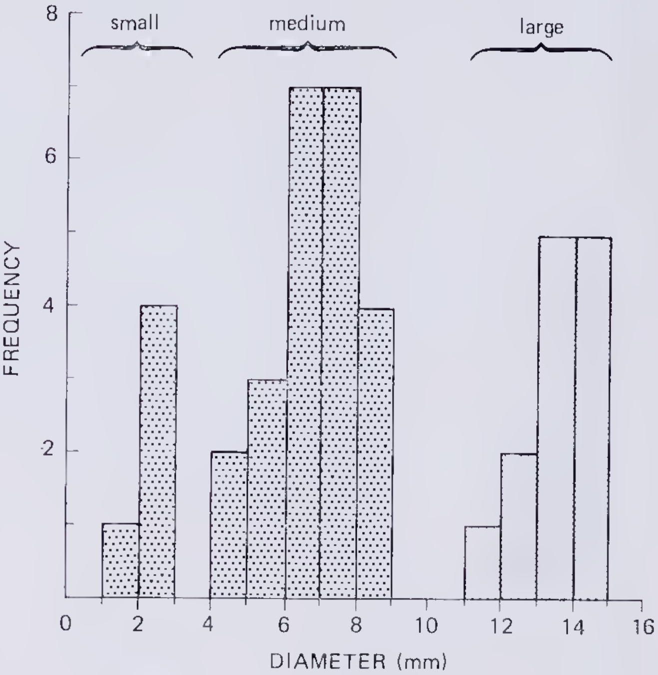

Figure 1.—Frequency distribution of diameters of aggregated dispersal units of *Acacia cyclops* from Western Australia. The largest diameter units were regurgitated pellets, the others faeces.

At Perth, silvereyes and singing honeyeaters (*Meliphaga virescens*) were netted and excreted intact seed of *A. cyclops*; at Eyre, silvereyes and brush bronzewing pigeons (*Phaps elegans*) have been reported to excrete seeds (Congreve. *pers. comm.)*; and at Two Peoples Bay Nature Reserve, birds taking seed were silvereyes, red wattlebirds, grey currawongs and Australian magpies (*Gymnorhina tibicen*). Birds observed defaecating seed at Two Peoples Bay were the grey currawong (L. D. Gill, *pers comm.*) and the magpie. The grey currawong also regurgitated seed-filled pellets (G. Folley, *pers. comm.*): its close relative, the pied currawong (*Strepera graculina*) in eastern Australia regurgitates pellets too. Currawongs were absent from Perth and singing honeyeaters were absent from Two Peoples Bay.

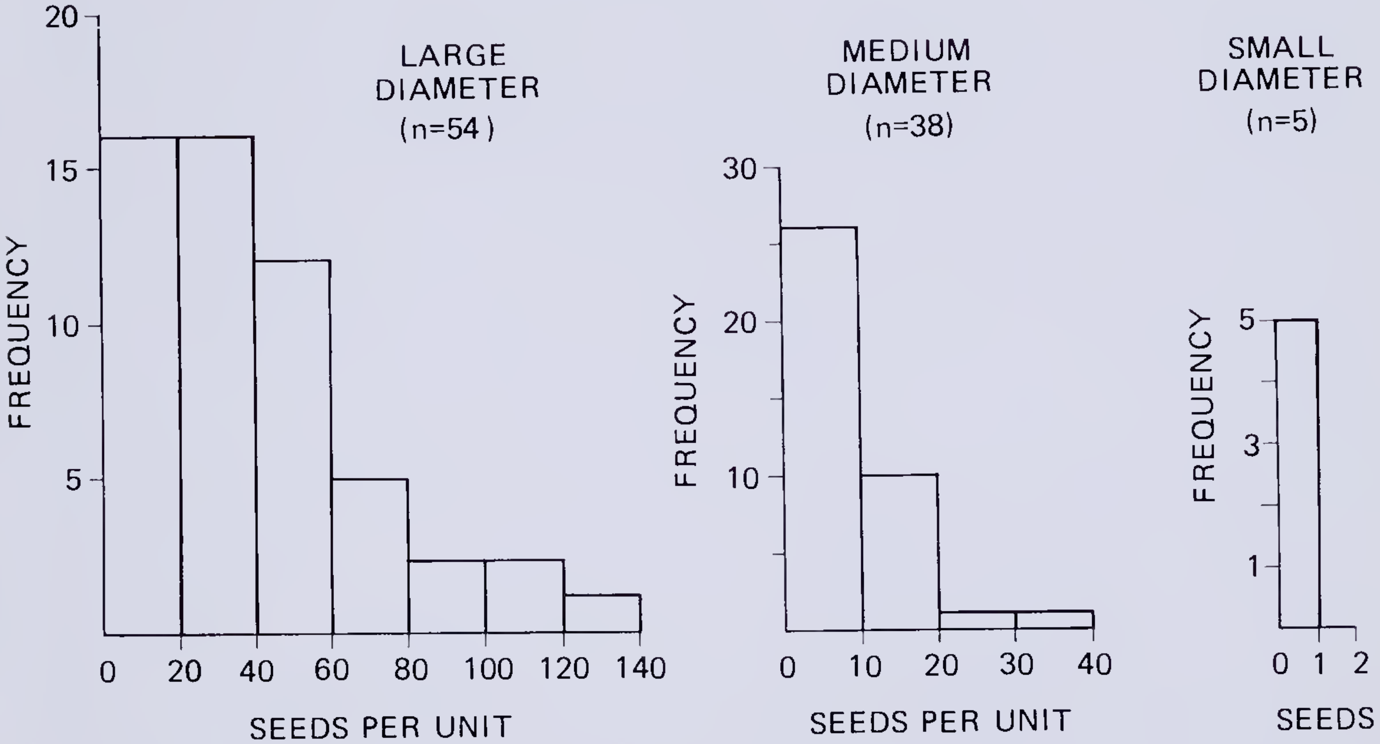

Figure 2.—Numbers of seeds per dispersal unit. The large diameter units were pellets, the others faeces.

The frequency distributions of pellets and faeces in relation to nearest possible source of seed was studied by walking transects along roads and tracks and in the picnic area at Two Peoples Bay i.e. following the distribution of plants (Fig. 3). Supplementary data on faeces came from Cape le Grand National Park. Pellets showed an hyperbolic distribution with distance from the nearest bush while the medium-size faeces, on the other hand, showed a peak associated with perch locations such as rocky outcrops, beneath overhanging branches and close to water points: the peak at 90 m was largely due to a collection made at Cape le Grand National Park. The smallest diameter faeces with single seeds were found only under bushes after intensive searching: the large *Acacia* seed tended to be poorly attached to the faecal unit.

Seed on the ground, whether aggregated or not, may be further transported. Grey currawongs, for example, will take arillate seed from the ground. Lizards (*Tiliqua rugosa*) and small mammals (*Rattus fuscipes*) were other possible dispersal agents. *Tiliqua* took *Acacia cyclops* seed in the laboratory and excreted it up to 2 weeks later (O'Dowd, *pers. comm.*) but a single dissection in the field revealed no seed. Similarly, a single *R. fuscipes* trapped under *Acacia cyclops* had no seed in its alimentary tract although there is circumstantial evidence that this species may take seed in the field (A. Baynes, *pers. comm.* and P. Christensen, *pers. comm.*). More obvious than vertebrate removal of seeds is invertebrate removal.

A number of invertebrates were attracted to seeds and arils of *A. cyclops* including beetles, bugs, grasshoppers and ants. Only ants commonly moved seed. At Two Peoples Bay, frequent observation of 32 seed placements each of 3 arillate seeds were made during daylight in January 1983 over a period of 4 days. Any seed removed was replaced. Activity of ants around seeds varied widely from place to place and time to time and involved a number of species (Appendix 1). Seed was either left alone, had its aril removed *in situ*, was transported short distances (e.g. a few cm or dm), was dropped in favour of other materials, or was transported into nests up to 2 m from point of collection.

Seed in loose currawong pellets was moved by ants occasionally but seed in cemented faeces seemed immobile. Breaking up dry faeces allowed ants to move this seed, with mostly-destroyed arils, to nests. Artificially supplying 40 fresh arillate seeds to a nest of *Melophorus* sp. in Perth followed by nest excavation the following day showed that seeds were placed at depths from 2 to 20 cm but mainly between 6 and 12cm. Five excavations 20 cm × 20 cm square and 12 to 20 cm deep under bushes of *Acacia cyclops* at Swanbourne, Perth, showed seeds in the profile but no obvious preferred depth: seeds below the surface lacked arils. Fresh seeds placed on small wooden trays, 10 seeds per tray, replicated 5 times at 3 sites with and without arils were all removed from the Swanbourne site within a week in November 1982.

At Two Peoples Bay, the fate of seed on the soil surface was studied on a poorly vegetated firebreak about 5 m from, and parallel to, a gravel road lined with bushes of *Acacia cyclops*. Seeds were placed on small wooden trays (63 mm square and 6 mm thick with a central circular depression 2 mm deep and 38 mm diameter) either under wire mesh cages (*ca* 130 mm square and 70 mm deep of mesh size

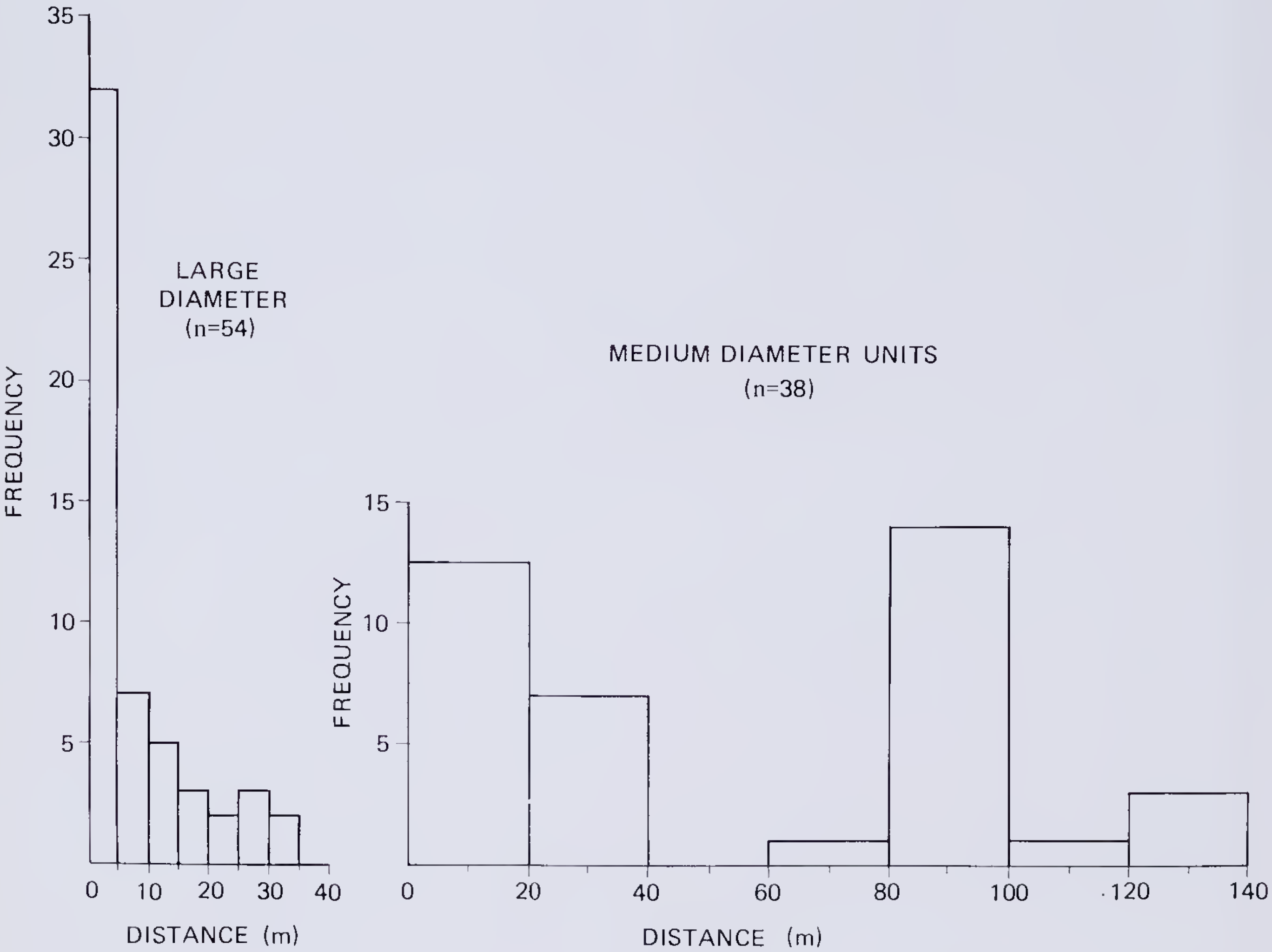

Figure 3.—Distances of dispersal from the nearest source of seed.

about 14-18 mm)—to deter birds and other vertebrates—or in the open, and either surrounded by a ring of sticky gel on the border of the wooden tray—to deter ants particularly—or left clean. On each tray were placed 10 seeds with arils or 10 seeds which had had most of the aril removed by ingestion and regurgitation by currawongs. The treatments were replicated 5 times at 5 locations about 10 m apart.

Ants were observed removing seed from trays, and bird tracks and a pellet consistent with currawong presence was seen next to affected trays. Uncaged arillate seed protected by gel tended to be lost all at once from any one replicate: at the same time all remaining arillate seed from other uncaged treatments also disappeared in four of the five replicates—consistent with removal by birds.

At the end of this three day experiment, 60% of the arillate seed had been removed but only 16% of the seed without arils had gone. The gel inhibited removal as only 23% of seed was removed from these treatments whereas 55% of seed on "clean" trays had been taken. The smallest difference between contrasting treatments was between caged and free seed: only 27% seed was removed from caged treatments and 50% from free. When combinations of treatments were compared the largest contrast was between the arillate seeds without gel protection (91% removal) and non arillate seed with gel (4% removal). Caged seeds with gel protection also lost 4% of seed (total), this loss being the seed removed by wind or by ants crossing the gel barrier after "bridges" of leaves and wind-blown sand had formed.

Three other experiments of this type showed similar removal rates by ants but presumed bird-removal rates were rather erratic depending on foraging success. Despite these results showing rapid removal of seed from trays, bushes with abundant arillate seed beneath them were easy to find. In these cases, one can infer the operation of one or more processes such as local exclusion of efficient dispersers by aggressive but less active foragers of *Acacia* seed (such as magpies), frequent disturbance of birds by motor vehicles, satiation of foragers or the absence of granivorous ants.

Seed dispersal and predation

Seed dispersal may enhance chances of seed survival in the presence of seed predators. A dispersal agent may remove the seed from the predator's habitat before predator attack or kill any predators in seeds before seed damage was lethal (as in the case of bruchid-attacked *Acacia* seed when dispersed by mammals in Africa—Lamprey *et al.* 1974). Predation of seeds was studied largely at Swanbourne (Perth) and Two Peoples Bay but observations were also made at Eyre.

Predispersal seed predation

Birds were major predators of immature seed at Eyre but not at the other study sites. Large pink cockatoos (*Cacatua leadbeateri*) virtually destroyed seed crops of individual bushes at Eyre in spring 1982. However, this damage was not severe enough on a population basis to prevent a prolific set of seed by many individual *A. cyclops* (P. Congreve, *pers. comm.*).

Insect predators of rapidly developing seed in spring were abundant at Swanbourne. In particular, bugs, weevils and moths were noticeable. The green hemipteran shield bug, *Coleotichus* sp. (prob. *C. costatus*, family Scutelleridae), and the brown, and much more streamlined Alylidid bug *Riportus* sp. (Van den Berg 1980 *b*) were common and fed on seeds within legumes (before dehiscence) and on seeds still in their legumes directly following legume dehiscence. Local swarms of the red and khaki nymphs of Pentatomid bugs, probably *Dictyotus* spp. (Van den Berg 1980 *b*) had a similar feeding behaviour. Evidence of attack of all these bugs was obtained by direct observation or from the small translucent "turrets" left upon withdrawal of their feeding tubes from the seed. "Turrets" were truncated cones of material with a cylindrical hole passing through their centres into the seed (or legume). They were *ca* 0.3 mm tall for the adult bugs and had a hole of about 0.03 mm which passed through the seed coat. Usually 1 to 7 "turrets" were found on affected seeds but up to 19 were observed. Holes through immature (green) testas tended to close but those in drier mature (black) testas tended to persist.

Larvae of weevils and moths affected dispersal by attaching seed to the pod wall or by binding the pod walls together thereby preventing dehiscence. Weevil larvae (*Melanterius* spp.) hatched from eggs inserted onto the surfaces of developing seeds within pods in spring. Eggs were abundant but not all hatched to larvae. Larvae fed on single seeds and completely consumed them. Their life cycle seemed short as the larvae fell to the ground and pupated before active dispersal of seed occurred (Van den Berg 1980 *a*). By contrast, larvae of the seed-feeding lepidopteran *Xerometra crocina* were found in the legumes of the previous seasons crop even while the present season's legumes were maturing rapidly in spring.

Post dispersal seed predation

Seed on the ground beneath bushes was not immune from attack. Bugs were particularly common. Of major importance was the shield-type bug *Adrisa* sp. (Cydnidae), a chocolate brown to black insect (when mature) found in the litter and upper soil layers under *A. cyclops* bushes at Eyre, Albany and Perth. Small sleek *Riportus* sp. (Alydidae) seen feeding on seeds at Two Peoples Bay were also pitfall-trapped at Swanbourne. Bugs were not found in 15 soil excavations (20 cm × 20 cm × 20 cm) at 5 m from bushes of *A. cyclops* in open ground at Two Peoples Bay but 12 of 15 samples from under 15 bushes had *Adrisa* in litter or soil with an average of 3 insects per sample.

Dispersal and germination

Dispersal of seed may cause it to be exposed to summer soil temperatures commonly of 60°C although these may only persist for short periods each day (Taylor 1981). In litter under bushes, this peak is unlikely to be reached and temperature fluctuations would be expected to be moderate. The large fluctuations and high temperatures of open ground may be expected to improve germination rate by analogy with behaviour of *Trifolium subterraneum* in the same region (Taylor 1981). Passage through birds and predation by bugs could also enhance germination through damage of the seed coat. Two germination experiments assessed these possibilities for *A. cyclops*.

Temperature treatments were applied to dry seed with and without arils using 50 seeds per Petri dish and 3 replicates of each treatment. For 8 days the seeds were exposed to a constant temperature of either 15°C or 60°C or given repeated half day exposures of 15°C followed by 60°C. After treatment the seeds were placed on moist filter papers in the laboratory and observed for 4 weeks. Of the 900 seeds used, 208 had germinated after 4 weeks: 49% of these had arils, 51% did not. Replicate results for any one temperature treatment did not overlap those for any other treatment. Means were 6% for 15°C treatment, 21% for 60/15°C and 42% for the 60°C treatment, thereby indicating a close correlation between time of exposure to 60°C and germination percentage and no effect of fluctuating temperatures.

Limited supplies of seeds were available from faeces, pellets and from fresh seed with evidence of feeding by bugs (viz. "turrets"). Three replicates of 50 seeds from faeces and the same numbers affected by bugs or unaffected—all from Perth—were placed in Petri dishes on moist filter paper at 20°C in a constant-temperature room. Similarly, seeds from droppings and pellets were compared with seeds taken directly from bushes at the Two Peoples Bay site. All of these comparisons continued for 120 days. Seeds from faeces at the Perth site germinated similarly to the control—near 60%—while seeds with "turrets" showed about 20% germination only. Seeds from faeces and regurgitated pellets from Two Peoples Bay showed about 80% germination while the controls gave about 15% only.

Discussion and conclusions

The weedy nature of *Acacia cyclops* which has become so evident in South Africa is apparent in its native land as well. In Australia it is often a species of disturbed areas, has abundant seed production, is quick growing and has effective dispersal mechanisms. Human dispersal and human disturbance as well as deliberate cultivation have expanded the distribution of the species and in some localities it is difficult to decide whether or not the species is a local escape from cultivation, is a chance introduction, or is indigenous to the area. With overseas interest in the species as a firewood crop (Ayensu *et al.* 1980), its possible use in Australia as a sand binder, and with further human disturbance in its natural area of occurrence, *Acacia cyclops* is likely to become even more prominent than at present.

Weeds tend to have generalist dispersers and this is true of *A. cyclops*. The avian dispersers identified in this study are all very widespread birds with opportunistic diets of various seeds and insects (for most) and nectar (for a few). Even the peripheral vertebrate possibilities—*Rattus fuscipes* and *Tiliqua rugosa*—are very widespread. Distributions of all these vertebrates extend well beyond the range of *Acacia cyclops.*

This study has suggested that regurgitation of seeds by currawongs is an important aspect of dispersal that differs in its pattern from that of avian faeces. Dispersal by regurgitation seemed to be associated with feeding patterns while dispersal in faeces had a strong component associated with perching behaviour. Scattered pellet material has been found near artificial watering points, however. In South Africa, the regurgitation mechanism has not been identified but patterns of *seedling* distribution have been interpreted in terms of perching behaviour of birds and distance from the presumed source (Glyphis *et al.* 1981) as in this study with *seeds.*

Seeds that have passed through birds have been found previously to germinate more rapidly than controls in South Africa (Glyphis *et al.* 1981) although present results were variable. This variability may deserve closer scrutiny and may be associated more with time exposed to the sun in the field than actual passage through the bird. Higher temperatures of seed dispersed onto open ground may increase rate of germination so that the response observed may depend on the time the seeds are left in the open before collection. Another factor may be the rate of passage through the bird. For pellets from currawongs, the seeds in some cases were associated with macerated arils while in others the arils were largely unaffected. Effects of passage through the complete digestive system may also vary according to speed—affected by type and amount of food ingested—and the nature of the gizzard. Birds which are usually predators of ripe seed (with strong gizzards) may pass only a few or no intact seed while seed dispersers (with softer gizzards) may pass a greater proportion. The boundary between predators and dispersers of ripe seed may not be clear cut. The same may be true for ants.

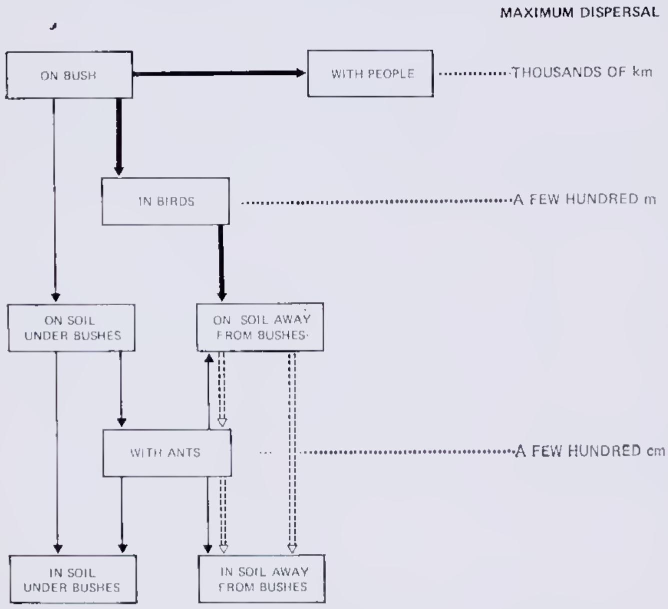

Figure 4.—A simplified summary of the processes of dispersal of *Acacia cyclops* in Australia. The thicker arrows represent what appear to be major paths for dispersal and successful establishment. The importance of burial at sites away from bushes is not known (dotted lines).

Ants showed varying interest in the seed-plus-aril combination and seemed much more concerned with the latter rather than the former part of this dispersal combination. Their activity served to bury the seed in some cases and scatter it in others. Distances of dispersal were small but position of dispersal could be significant. Burial in the nest may protect it from predators and even provide a more nutrient-rich environment in which to grow.

The heterogeneity in the distribution and abundance of predators and dispersers was marked. Predation of unripe seed by cockatoos was prevalent at Eyre but absent at other study sites; canopy feeding by bugs was more common at Swanbourne (Perth) than at Two Peoples Bay; currawongs were present at Eyre and Two Peoples Bay but absent from Perth; and, at a local level, the dispersion and types of seed-collecting ants varied widely. Ants were slower but more consistent in removal of seed from the ground than birds which were erratic in their discovery and ingestion of seed.

Three scales of dispersal distance were detected in this study. People moved seeds locally but also up to thousands of kilometres. Birds moved seeds distances of the order of hundreds of metres from the nearest possible sources; and ants moved seed up to 2 m (Fig. 4). Each level may be important to the spread and establishment of *Acacia cyclops:* people allowed the species to spread beyond Australia, birds have dispersed the seeds to newly-disturbed sites and ants have buried seeds. The details of dispersal are numerous and concern many species across the range of *Acacia cyclops:* a simplified view of this process is depicted in Fig. 4.

Optimum chances of germination and seedling establishment seem to be associated with bird dispersal to bare unshaded soil early in the dispersal season. If the seed was dispersed early it had a greater chance of avoiding predation by hemipteran predators. Populations of predatory bugs seemed to increase through spring and summer thus predisposing late maturing seeds to greater attack. Their feeding reduced viability of seed. Early in the season, the supply of mature seeds to bird dispersers was limited and eagerly sought: later, the crop was abundant and the chances of quick dispersal seemed diminished. If deposited after passage through a bird, germination of seed could be enhanced: when food was abundant the time spent internally was likely to be minimal. Deposition in full sun may have enhanced germination. If the seed was dispersed away from the host plants of predatory *Adrisa,* the chances of establishment were again likely to be improved. Evidence for these conclusions has sometimes been indirect but the stage is now set for the direct test of these ideas.

Acknowledgements.—Permission was gratefully received from Majors A. D. Craig and T. White of the Australian Army to work in the Army area at Swanbourne (Perth), from the Director of the Western Australian Department of Fisheries and Wildlife to work at Eyre and Two Peoples Bay, from the Royal Australian Ornithologists' Union also to work at Eyre and from the National Parks Authority to collect seed from Cape le Grand National Park near Esperance, W.A. Mr. and Mrs. P. Congreve of Eyre Bird Observatory and Mr. G. Folley, the Ranger at Two Peoples Bay Nature Reserve were particularly helpful. Dr. R. Wooller and Mr. D. Hamley of Murdoch University kindly carried out mist netting and identification of birds at Swanbourne. Dr. R. W. Taylor CSIRO Division of Entomology provided authoritative ant identifications while his colleagues Dr. I. B. Common and Dr. T. Weir kindly identified moths and bugs respectively. Dr. A. Baynes, Western Australian Museum gave advice on small mammals and dispersal. Mr. A. Hopkins, Department of Fisheries and Wildlife gave valuable logistic support. Office space and laboratory facilities were supplied by Dr. F. J. Hingston and Mr. R. Perry of CSIRO Laboratories, Floreat Park (Perth). Dr. D. J. O'Dowd Flinders University of South Australia was a source of particular encouragement.

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Appendix

Ants observed in association with seeds of *Acacia cyclops* in Western Australia.

Dolichoderinae	
Iridomyrmex sp.[1,2]	(carried seed-plus-aril).
Formicinae	
Camponotus sp.[2]	(carried seed-plus-aril).
Melophorus spp.[1,2]	(two species either removing arils from seeds or carrying the seed-plus-aril combination).
Myrmicinae	
Monomorium sp.[1]	(tiny ants which cut arils into tiny pieces for transport and only inadvertently moved seeds a few cm at most).
Pheidole sp.[1,2]	(removed arils and carried them away or moved whole seed-plus-aril unit).
Ponerinae	
Rhytidoponera spp.[1,2]	(two species carrying seed-plus-aril units).

[1] See also Berg (1975); Berg classified his *Camponotus* spp. as non-collectors.

[2] See also Majer (1982).